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THE UTILISATION OF FOOD BY CERTAIN LEPIDOPTEROUS LARVAE

By A. C. Evans.

(*Rothamsted Experimental Station, Harpenden, Herts.*)

(Read 1st March, 1939.)

In a previous paper, Evans (1939), the utilisation of food by the larva of *Phalera bucephala* (L.) was discussed. In the present paper further results on *P. bucephala*, fed on Hornbeam (*Carpinus Betulus*), *Malacosoma neustria* (L.) fed on Willow (*Salix viminalis*), *Aglais urticae* (L.) fed on Nettle (*Urtica dioica*) and *Pieris brassicae* (L.) fed on Cabbage (*Brassica oleracea capitata*) are given.

The same methods of chemical analysis of food and excreta have been used here as in the previous work (except where noted) but the methods of studying the utilisation of food have been much elaborated in order to study the problem more fully.

Biological Methods.

The comparative experiments on larvae in the last instar were carried out in airtight tins 6 inches in diameter and 6 inches in height. A quantity of undamaged leaves of similar age were well mixed and divided into 4 batches. Each batch was weighed and one dried immediately at 100° C. The other batches were placed in tins, one being used to estimate the natural loss in weight due to respiration and evaporation, the other two to serve as food for the larvae. The larvae were divided into 5 batches [1] and weighed. One batch was dried immediately, 2 batches were placed in tins containing food and the other two in empty tins. At the end of the experiment the control leaves were weighed and dried. The natural loss of water and dry matter can be calculated from these figures as the original amounts present may be estimated from the known initial percentage dry weight. The larvae and excreta in both the starved batches were then weighed; the excreta and one set of larvae were dried, the other set of larvae was allowed to continue excretion and the excreta collected, weighed and dried at intervals until excretion ceased. From the data obtained the loss of water and dry matter can be calculated. Also an estimation of the amount of material initially present in the alimentary canal can be made in terms of excreta. A more accurate determination of the contents of the alimentary canal would probably prove extremely difficult because of the presence of food in all stages of digestion and of the digestive secretions. The weights of the fed larvae, food remains and excreta were then determined. The food remains, excreta and one batch of larvae were dried, the other batch of larvae was allowed to continue excreting without food and the excreta collected, weighed and dried at intervals until excretion ceased. The difference in weight between the initial and final amounts of " excreta equivalents " of the alimentary canal contents was subtracted from the increase in weight of the larvae; in this way a more accurate estimation of the amount of growth was made.

[1] 25-40 larvae per batch.

From the data obtained, a fairly complete account may be drawn up of the amount of food consumed and the amount utilised; of the latter the fraction used for growth is known, the remainder is probably used for energy production.

To facilitate discussion of the results, certain coefficients are designated and defined as follows.

$$\text{Coefficient of utilisation, } Q^{U}F,D \text{ or } W = \frac{\text{Weight of food utilised}}{\text{Weight of food consumed}}.$$

$$\text{Coefficient of growth, } Q^{G}F,D \text{ or } W = \frac{\text{Increase in weight of larvae}}{\text{Weight of food utilised}}.$$

$$\text{Coefficient of Metabolism, } Q^{M}F,D \text{ or } W = \frac{\text{Weight of food utilised—increase in weight of larvae}}{\text{Weight of food utilised}}.$$

F = fresh food. D = dry matter. W = water.

Taranukha (1937) has defined a coefficient of assimilation for *Lymantria dispar* (L.) as the amount of food required to produce one gram of excreta; this is very similar to $Q^{U}F$ as defined above.

A complete set of data obtained for *A. urticae* is given in Table I. It will be seen that the corrections introduced for the natural loss of weight of the food during the experiment, and for the " excreta equivalent " of the alimentary

TABLE I.

Data obtained for the study of the utilisation of food of *A. urticae*, 40 larvae.

		Weight in grammes		
		Fresh	Dry Matter	Water
	Food records.			
A.	Loss in weight of food given . . .	4·857	1·381	—
B.	Natural loss in weight	0·040	0·033	—
C.	Food consumed (A — B)	4·817	1·348	3·469
D.	Excreta eliminated during experiment . .	3·080	0·890	—
E.	Excreta eliminated after experiment . .	1·326	0·284	—
F.	Total (D + E)	4·406	1·174	—
G.	" Excreta equivalent " of alimentary canal contents at beginning of experiment . .	0·729	0·173	—
H.	Excreta produced during experiment (F — G)	3·677	1·001	—
I.	Food utilised (C — H)	1·140	0·347	0·793
	Feeding Metabolism.			
J.	Increase in weight of larvae	1·266	0·329	—
K.	" Excreta equivalent " at end of experiment .	1·326	—	—
G.	Excreta equivalent at beginning of experiment	0·729	—	—
L.	Increase in " excreta equivalent " (K — G) .	0·597	—	—
M.	Increase in living matter J — L . . .	0·669	0·218	0·451
	Food unaccounted for (I — M) . . .	0·471	0·129	0·342
	Starving metabolism.			
	Decrease in weight	0·600	0·149	—
	Excreta lost	0·369	0·101	—
	Decrease in living matter	0·231	0·048	0·183

canal contents at the beginning and end of the experiment, are essential for the accurate determination of the various coefficients.

It was not feasible to carry out a detailed study of the type described above in a preliminary study to determine whether any variation in the values of the coefficients occurs during the larval stages. A more simplified but comparatively accurate method was used. Larvae of *P. bucephala* were given weighed amounts of food (Hornbeam leaves, *Carpinus Betulus*) in closed vessels and the food consumed, excreta produced and increase in weight of the larvae determined. The natural loss of weight of the food during the experiment was determined, also the initial percentage dry weight of the food and the dry weight of the excreta. No correction was made for the increase in weight of the alimentary canal contents as very large numbers of larvae would have been required for this. From the above data the weights of dry matter and water consumed and excreted could be determined and also the amounts of fresh food used for growth and metabolism.

Changes in the Utilisation of Food with Age.

Taranukha (1937) has shown that the larvae of *Lymantria dispar* utilise, in the early instars, more of the food consumed than they do in the later instars. The coefficient of assimilation is reduced from about 7 in the first instar to 3 in the last instar. Certain results of Hiratsuka (1926) also show a similar trend. This change has been studied in some detail during the first instar of *Smerinthus populi* (L.) fed on willow and throughout the larval stage of *P. bucephala*. The results on *S. populi* were obtained with a batch of 20 larvae; these were given fresh food every 24 hours. The results on *P. bucephala* were obtained with sample batches taken from a stock caged out of doors. The stock was kept comparatively uniform in age by rejecting those individuals which moulted early and those which moulted late, thus about 24 hours or slightly more separated the oldest and youngest larvae at the beginning of each instar.

Table II.

Food relationships of 1st instar larvae of *S. populi*.

Day:	1	2	3	4	5	6	7	8	9	10
Coefficient of utilisation . . .	0·925	0·741	0·621	0·564	0·558	0·565	0·586	0·521	0·498	0·528
Consumption in gm. per gm. of larva per day . .	0·663	0·745	0·629	0·546	0·391	0·459	0·409	0·390	0·320	0·214
Utilisation in gm. per gm. of larva per day . .	0·613	0·555	0·385	0·308	0·218	0·259	0·240	0·203	0·159	0·113
Metabolism in gm. per gm. of larva per day . .	0·500	0·350	0·137	0·098	0·074	0·096	0·108	0·063	0·056	0·053
Coefficient of growth	0·155	0·370	0·644	0·681	0·661	0·629	0·546	0·629	0·649	0·545

Accurate results on the utilisation of dry matter were not obtained for *S. populi* as only small amounts of food were consumed and the amount of dry matter present in the food could not be calculated with sufficient accuracy owing to the great variability in the percentage dry weight of the individual leaves. By feeding half-leaves to large numbers of 1st, 2nd and 3rd instar larvae of *P. bucephala* and using the opposite half-leaves in part as controls for

determining natural loss of weight and in part for the determination of the initial percentage dry weight, accurate results have been obtained for the consumption and utilisation of dry matter and water. For the 4th and 5th instars, large quantities of whole leaves were used.

The Q^UF for the 1st instar larva of *S. populi* falls off rapidly as the larva increases in size, at the end of the instar being only about half of what it was at the beginning. The consumption, utilisation and metabolism of food per gramme of larva per day also fall off rapidly, the last-named especially so, its final value being only one-tenth of its initial value. The Q^GF increases rapidly until the 4th day, after which it remains more or less constant.

In *P. bucephala* Q^UF, Q^UD and Q^UW fall steadily during the 1st and 2nd instars and afterwards increase and fluctuate irregularly. The consumption, utilisation and metabolism of food per gramme of larva per day follow a similar course. The Q^GF increases until the middle of the 3rd instar and then fluctuates irregularly.

In spite of the natural variations in the composition of the food due to age and varying weather conditions it is considered that the initial falls in the coefficients of utilisation and metabolism and in the consumption and utilisation per gramme per day are significant and are due to a factor or factors intrinsic in the larva itself. The interpretation of results on dry matter is complicated because the dry matter is a complex of substances the concentration of any one of which may at different times determine the rate of consumption, etc., of food. Evans (1938) found that larvae of *Pieris brassicae*, when fed on cabbage

TABLE III.

Food relationships of larvae of *P. bucephala*.

Day:	1	4	7	14	18	23	24	26	32	41	45
Instar:	1	1	1	2	2	3	3	3	4.	5	5
Coefficient of utilisation:											
Fresh food	0·753	0·724	0·626	0·474	0·385	0·355	0·464	0·445	0·462	0·499	0·414
Dry matter.	0·235	0·251	0·225	0·185	0·174	0·173	0·237	0·238	0·240	0·156	0·226
Water	0·973	0·966	0·855	0·709	0·559	0·532	0·668	0·615	0·655	0·791	0·610
Consumption in gm. per gm. of larva per day:											
Fresh food	0·541	1·095	0·978	0·907	0·777	0·569	0·869	0·932	0·757	0·665	0·599
Dry matter.	0·160	0·373	0·350	0·407	0·359	0·280	0·412	0·420	0·352	0·283	0·261
Water	0·381	0·722	0·628	0·500	0·418	0·289	0·457	0·512	0·405	0·382	0·338
Utilisation in gm. per gm. of larva per day:											
Fresh food	0·408	0·793	0·612	0·430	0·298	0·202	0·404	0·425	0·462	0·331	0·248
(A) Dry matter	0·038	0·094	0·080	0·076	0·062	0·049	0·097	0·101	0·114	0·048	0·058
(B) Water	0·370	0·699	0·532	0·354	0·236	0·153	0·307	0·324	0·348	0·290	0·190
Metabolism in gm. per gm. of larva per day:											
Fresh food	0·369	0·625	0·418	0·250	0·137	0·082	0·092	0·145	0·128	0·214	0·123
Coefficient of growth	0·100	0·211	0·320	0·417	0·537	0·592	0·785	0·650	0·728	0·329	0·502
Ratio A : B	9·7	7·4	6·6	4·6	4·8	3·1	3·2	3·2	3·1	6·1	3·3

leaves which had been kept under poor conditions of light for 24 hours, consumed much more than when fed on normal leaves. The leaves kept under poor conditions of light had a lower carbohydrate content than the controls. A further complication is the change in feeding habits of the larva as it grows larger. The 1st instar larva nibbles its food between the small cross veins of the leaf, rarely biting through the leaf. The 2nd instar larva bites clean through the leaf, consuming the small cross veins but not the secondary veins, while the 3rd instar larva can bite through the tips of the secondary veins; later instars can demolish practically the whole of the leaf. Thus as the larva grows older it consumes food with a higher content of indigestible matter, since

Evans (1939) has shown that cellulose and hemicelluloses are not utilised by the larva of *P. bucephala*. The coefficient of utilisation recorded above is based on the assumption that the percentage dry matter in the actual food consumed is the same as that of the food given. This assumption is not quite justified for the 1st, 2nd and 3rd instars which consume the softer portions of the leaf tissues. What therefore will be the effect of this increasing proportion of indigestible matter in the food on Q^UD? An attempt was made to answer this question by estimating the amount of cellulose in the food and excreta for the first four instars and recalculating Q^UD on a basis of cellulose-free food and excreta. Not enough material was available to carry out the analysis on each separate collection of excreta so all the material from each instar was analysed in one batch. The results obtained suggest that the fall in Q^UD during the 1st and 2nd instars is not solely due to an increase in the amount of indigestible matter in the food as shown in Table IV.

TABLE IV.

The effect of indigestible matter on the coefficient of utilisation of dry matter.

Instar:	1	2	3	4
Original data . .	0·235	0·177	0·254	0·240
Cellulose-free data .	0·203	0·160	0·274	0·302

A further study of the utilisation of food along these lines might give a more accurate account than the cruder methods used in this study.

In the case of water there can be no doubt that the fall in Q^UW is significant. The extraction of water from the food during the first four days of larval life is remarkably efficient. If the ratio of dry matter utilised per gramme of larva per day to water utilised per gramme per day is worked out, it is found that it falls until the beginning of the 3rd instar and then remains constant (except for one aberrant value), Table III. In the case of the American Tent-caterpillar (*Malacosoma americana* (Fab.)), Rudolfs (1926) has shown that immediately after hatching the percentage water content of the larva increases rapidly, then more slowly, and finally remains constant. These changes in the water content of the larva might be explained on the basis of the change in ratio of dry matter to water utilised.

COMPARATIVE OBSERVATIONS.

Table V shows that the larvae of different species utilise and consume food at very different rates. Two sets of data are given for *P. brassicae*, the one obtained on the leaves of young plants and the other on the outer leaves of mature plants. The utilisation and consumption of food differ in this case. Unfortunately not enough larvae were available to study the Q^GD and Q^GW. The Q^GF does not differ very greatly in the four species. The metabolism per gramme of feeding larvae per day is about the same for *M. neustria* and *P. brassicae* but is very much higher in *A. urticae*. A similar difference is found in the metabolism of starving larvae. The difference lies mainly in the amount of water evaporated. There appears to be a definite relationship between the Q^UW and the water content of the food (fig. 1). This graph is based on the data in Tables III and V. There does not seem to be any relationship between the Q^UD and the percentage dry matter in the food. This result is to be

expected since the various constituents of the dry matter are utilised in the different proportions (Table VI).

TABLE V.

Comparative observations on the utilisation of food.

Species:	*M. neustria*	*A. urticae*	*P. brassicae* [2]	*P. brassicae* [3]	*P. bucephala*
Mean weight of larva in gm.	0·393	0·212	0·353	0·358	—
% Dry weight of larva	17·7	17·4	—	17·2	—
% Dry weight of fresh food	37·3	28·2	10·7	12·8	43·7
Coefficient of utilisation:					
Fresh food	0·327	0·237	0·205	0·236	0·490
Dry matter	0·340	0·257	0·363	0·391	0·350
Water	0·319	0·229	0·185	0·214	0·603
Coefficient of growth:					
Fresh food	0·678	0·587	0·668	0·664	0·562
Dry matter	0·408	0·622	—	—	—
Water	0·854	0·569	—	—	—
Consumption in gm. per gm. of larva per day:					
Fresh food	0·861	2·074	2·047	1·504	1·006
Dry matter	0·326	0·581	0·233	0·188	—
Water	0·535	1·493	1·813	1·316	—
Utilisation in gm. per gm. of larva per day:					
Fresh food	0·282	0·491	0·420	0·354	0·496
Dry matter	0·111	0·149	0·085	0·073	—
Water	0·171	0·342	0·335	0·281	—
Metabolism in gm. per gm. of larva per day:					
Fresh food	0·091	0·203	0·111	0·119	0·218
Dry matter	0·066	0·056	—	—	—
Water	0·025	0·147	—	—	—
Starving metabolism:					
Living matter	0·025	0·105	0·045	—	—
Dry matter	0·016	0·022	—	—	—
Water	0·009	0·083	—	—	—

[2] Data obtained on young leaves.
[3] Data obtained on old leaves.

Enough excreta was not available for a detailed analysis of the type carried out by Evans (1939). In this study, therefore, the analytical procedure was modified. Owing to the great loss of fructose on clearing the soluble sugar extract with dibasic lead acetate, Van Plank (1936), the extract was not cleared before analysis; the reducing substances present are reported as glucose. Uric acid and ammonia were not estimated so that the difference in the nitrogen contents of the food and the corresponding amount of excreta represents the amount retained by the insect and does not account for that fraction of the nitrogenous substances used in respiration. Also, no estimate can be made of the amount of non-protein nitrogen utilised; this probably is but small in the case of *M. neustria* and *A. urticae* but might be large in *P. brassicae*, the food of which has a low protein content. An examination of the results of Evans (1939) shows that the amount of protein utilised can perhaps be used as a fair measure of the amount of the nitrogenous substances utilised; his figures show 7·32 mg. of protein-N utilised and 0·24 mg. of non-protein N utilised.

The results given in Table VI show that the three species utilise a higher proportion of sucrose than of glucose; a similar result was obtained for *P. bucephala*, Evans (1939). *M. neustria* probably utilises starch but *A. urticae* and *P. brassicae* do not. On the other hand, *M. neustria* does not utilise fat

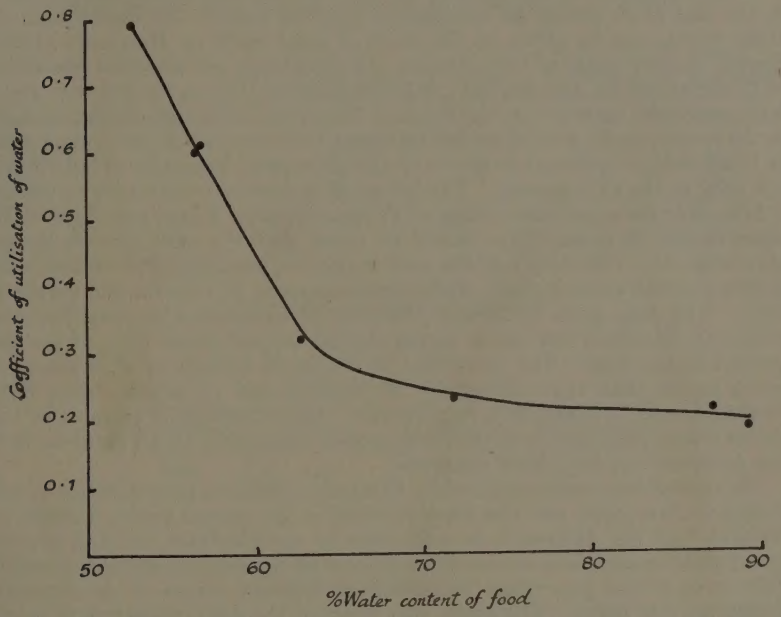

FIG. 1.—The relationship between the water content of the food and the coefficient of utilisation of water for four species of lepidopterous larvae in the last instar.

TABLE VI.

The utilisation of the chemical constituents of 1 gm. of fresh food, in mg.

	M. neustria		*A. urticae*		*P. brassicae*			
	Food	Utilised	Food	Utilised	Food [4]	Utilised	Food [5]	Utilised
Water . .	627	200	718	159	893	165	872	186
Dry matter .	373	127	282	72	107	39	128	50
Glucose .	19·2	12·2	4·2	2·1	3·8	2·2	—	—
Sucrose . .	19·1	16·8	7·7	5·6	0·8	0·5	—	—
Starch . .	8·6	3·0	11·2	1·0	4·6	0·0	—	—
Fat . .	6·6	1·8	10·3	5·7	—	—	6·0	4·8
Ash . .	30·4	8·3	38·8	− 2·7	—	—	18·7	1·2
Protein-N .	9·98	7·16 Retained	9·91	6·28 Retained	3·76	3·11 Retained	—	—
Total N .	10·81	3·12	11·19	4·54	4·71	2·61	—	—

[4] Data obtained on young leaves.
[5] Data obtained on old leaves.
Carbohydrates expressed as glucose.

to the same extent as the other two species. *P. bucephala* also utilises a high proportion of fat. Whether the utilisation of starch by *M. neustria* is correlated with its inability to utilise much fat or whether the fat of the willow differs from that of cabbage and nettle can only be decided by further study.

The proportion of ash utilised by the three species differs considerably; in the case of *A. urticae* an excretion of ash was found. An explanation for these results can be given on the basis of some work by Hiratsuka (1920). During the last instar of the silkworm, the percentage ash absorbed was about 30% during the 1st and 2nd days, it fell steadily to 11% on the 5th day, and a large excretion occurred on the 6th and 7th days. Although the larvae used in the present study were all in the last instar, they were not strictly comparable as to age within the instar as shown by the subsequent behaviour of individuals not used in the experiments. The larvae of *A. urticae* commenced to pupate 2 days after the experiment, those of *P. brassicae* after 4 days and those of *M. neustria* after 9 days. Thus it will be noted that the most mature larvae, *A. urticae*, were excreting ash, the next in order of maturity, *P. brassicae*, were utilising a small amount of ash, while the least mature, *M. neustria*, utilised about 25%. The data given by Evans (1939) for *P. bucephala* also show that the relatively immature last instar larvae studied utilised about 30% of the ash present in the food. The percentage of protein-N utilised by *P. brassicae* is much higher than that utilised by *M. neustria* and *A. urticae*, being 83% compared with 72% and 63% respectively. The % protein-N retained by the larvae differs considerably in the three species, being 20% for *M. neustria*, 40% for *A. urticae* and 55% for *P. brassicae*.

In view of the results obtained by Hiratsuka (1920) on the utilisation of ash during the last instar and also those obtained in the present study, it might be thought that the differences in utilisation of carbohydrate, fat and protein noted between the three species have little or no significance owing to possible differences in the percentage utilisation at different stages of development during the last instar. Hiratsuka also recorded the daily utilisation of crude protein, crude fat and nitrogen-free extract during the last instar. He found that the utilisation of these fractions does not show any great changes except for a decrease during the two days previous to cessation of feeding. It is therefore considered that the differences recorded in the present study indicate real differences in the utilisation of the various substances in the food supplied.

The comparison of the utilisation of natural food by phytophagous larvae of different species is rendered difficult because it is often impossible to feed the different species on the same food. It is considered that any comparison on the basis of the food offered is not likely to establish any broad differences between species owing to the wide variation in the chemical composition of the host-plant under various conditions of growth. The soundest basis of comparison which can be suggested now is the determination of the amounts of various substances utilised by a definite weight of larvae in a given time under standard conditions of temperature, humidity and light.

Table VII gives data calculated on this basis for four species. About 80% of the dry matter utilised is accounted for in the table. The composition of the dry matter utilised varies greatly in the different species, especially the ratio of protein to non-nitrogenous substances. Wood (1924) defines a ratio of digestible protein to digestible non-nitrogenous substances which might prove of value in comparative work. This ratio, the nutritive ratio, is obtained by multiplying the digestible fat by a factor 2·25, adding the digestible carbohydrate and then dividing this sum by the digestible protein. Fat is multiplied

by 2·25 because fat produces about 2·25 times as much heat as the same weight of carbohydrate. This ratio can be calculated from the results given in Table VI and show great diversity.

TABLE VII.

The utilisation of the chemical constituents of the food in mg. per gm. of larva per day.

	M. neustria	*A. urticae*	*P. brassicae*	*P. bucephala*
Total carbohydrates . .	27·5	16·0	5·5	49·0
Fat	1·5	11·8	7·2	8·4
Protein	47·4	100·3	49·0	56·6
Ash	7·1	0·0	1·8	9·9
Total . . .	83·5	122·5	63·5	123·9
Dry matter. . . .	111	155 [6]	approx. 79	157
% Accounted for . .	75	79	80	79

[6] Adjusted to allow for ash excretion.

TABLE VIII.

Nutritive ratios.

M. neustria	*A. urticae*	*P. brassicae*	*P. bucephala*
0·65	0·32	0·44	1·18

TABLE IX.

Comparative chemical composition of lepidopterous larvae and some herbivorous mammals on a fresh weight basis.

Species	% Dry weight	% Fat	% Carbo-hydrate	% Crude protein	% Ash	$\frac{\text{Fat} \times 2{\cdot}25 + \text{Carbohydrate}}{\text{Crude protein}}$
P. brassicae (own data) .	28	6·4	2·0	13·0	—	1·3
M. americana Rudolfs .	28	6·7	very small	14·7	1·8	1·0
B. mori Hiratsuka . .	22	3·4	2·0	14·7	1·1	0·7
Cattle 23 months, Armsby .	40·6	18·8	—	17·4	4·5	2·4
Steers ½ grown, Armsby .	38	14·0	0·5	19·2	4·6	1·6
Sheep 1 year, Armsby .	39	19·9	—	15·8	3·4	2·8

The nutritive ratios given above also differ widely from those determined for growing cattle, sheep and pigs; Shaw (1916) gives nutritive ratios of 4·7 to 7·0 for these animals. Wood (1924) gives nutritive ratios of 5·0 and 6·0 for milch cows fed on kale and cabbage respectively.

A partial explanation for the big differences between the nutritive ratios for lepidopterous larvae and some herbivorous farm animals can be given on a basis of the chemical composition of their tissues (Table IX). The data show

that the mammals contain much more fat, rather more protein and less carbohydrate than the insects. Thus they require a higher proportion of fat and carbohydrate to protein than the insects. If the ratio of fat and carbohydrate to protein in the tissues is calculated on the same basis as the nutritive ratio, it is seen that the ratio is much higher for the mammals than for the insects.

Summary.

The food relationships of the larvae of *Phalera bucephala*, *Aglais urticae*, *Smerinthus populi*, *Malacosoma neustria* and *Pieris brassicae* have been studied.

The coefficient of utilisation of food falls steadily during the 1st and 2nd instar of *P. bucephala*; during the 3rd, 4th and 5th instars it fluctuates irregularly. The consumption, utilisation and metabolism of food per gramme of larva per day follow a similar course. The coefficient of growth increases until the middle of the 3rd instar and then fluctuates irregularly. About 90% of the water contained in the food is extracted during the first four days of larval life.

The larvae of the species studied utilise and consume food at very different rates. The amounts of carbohydrate, fat and ash utilised per gramme of larva per day differ very much in the four species.

The nutritive ratio of the larvae is very much lower than that of certain growing mammals, *i.e.*, cattle, sheep and pigs, and the difference seems to be correlated with the chemical composition of the tissues.

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